

On the Cloacal Bladders and on the Peritoneal Canals in Chelonia.
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THE cloaca in the Chelonia, as is generally known, is an elongated saccular dilatation intervening between the termination of the rectum and the orifice at the base of the tail, or external anus, and into which certain important structures open. It is of considerable length and transverse capacity, and has exceedingly thin walls, and is directly continuous with the rectum. But on the floor, concealed by closely apposed folds is an anteriorly and downwardly directed dilatation or chamber, terminating in the orifice of the bladder, and having, opening on its lateral walls, the orifices of the seminal tubes or of the oviducts, according to the sex, and also the openings of the ureters. The folds which close in this chamber for the general cavity of the cloaca are backwardly continued to the base of the glans, enclosing the urino-genital groove. By this arrangement of the folds, the fæcal matter in its transit outwards is prevented from having access to the orifices of those important structures the generative organs and the kidneys, and to the urino-genital groove. In certain Chelonia another fold exists above and slightly posterior to the termination of the rectum, having above it on either side the large patulous openings of the cloacal bladders. This fold springs from either lateral wall of the cloaca; and those two segments of it meet in the mesial line and constitute an arched forwardly directed fold. In some species the centre of the arch is tacked to the roof of the cloaca by a narrow longitudinal fold or septum which divides the area which overlies the fold into two halves, into each of which opens a cloacal bladder; while in others the septum does not exist, and of course the area overlying the fold is continuous.

At the extremity of the urino-genital groove on the floor of the cloaca is the large glans of the penis, and in the opposite sex the identically formed but less developed clitoris. Springing from the sides and base of the glands is a crescentic fold of the mucous membrane, which passes backwards tending towards the mesial line to meet its fellow of the opposite side, thus constituting a hood or rudimentary præputium for the isolation of the glans penis or clitoridis from the fæcal matter of the common cavity of the cloaca, and thus simulating the structure of the Monotremes

and of some Struthious birds. The penial and clitorid portion of the cloaca in Trionychidæ and Emydidæ is richly coloured with a purplish-black pigment, which invests the whole of the glans and the hood or præputium and a considerable portion of the pillars of the penis and clitoris anterior to the glans. A similarly coloured pigment also occurs in the openings of the oviducts of some of the Trionychidæ. But in the Southern-Asiatic species of land-tortoise referable to the subgenus *Peltastes* the cloaca and the glans are devoid of black pigment, and are generally pale yellow. The glans penis appears to have a form peculiar to each leading group, and is doubtless in its construction specially adapted to ensure the most perfect efficiency of function in special relation to the habits of life of the animal. There is a terrestrial and there is an aquatic glans penis, the latter having essentially the character of a grasping organ.

It is not the object of this paper to describe the copulative organ, so far as the glans is concerned; but I may be permitted to remark that perhaps in no class of animals is the glans clitoridis so perfect a reproduction of the glans penis as in this most interesting group of vertebrates. So alike are they in young Chelonians, that a direct appeal to the peritoneal cavity is necessary to determine the sex.

Before I take up the question of the peritoneal canals and their relation to the other parts of the penis, the title of this paper necessitates that the cloacal bladders should be first described.

The anal pouches, or cloacal bladders, as they might be more properly called, were first accurately described by Bojanus*, in his account of the anatomy of the common Emyde of Southern Europe, *Emys europæa*; but since his day they do not appear to have received that attention which their importance apparently demands, and which is indicated by the circumstance that they occur in some of the well-marked types and are absent in others. They are the structural equivalents of the similar bladders or vessels which are met with in the crocodiles, and in most lizards and snakes, in various degrees of development; but they attain the highest differentiation in this group.

I have recently had the opportunity to examine a number of Asiatic species belonging to different genera; and I find that these bladders occur in *Emys trijuga*, *E. crassicollis*, *Batagur dhongoka*, *B. lineatus*, *B. fuscus*, *B. (Morenia) ocellata*, *B. (Morenia) bera-*

* Anat. Testud. europ. 1819-21.

morei, *Pangshura tecta*, *P. tentoria*, *P. smithii*, *P. flaviventris*, *P. sylhetensis*, *Cuora amboinensis*, *Cyclemys dentata*, *Geoemyda depressa*, *G. grandis*, and *Platysternum megacephalum*. In *Pangshura*, *Cyclemys*, *Platysternum*, and *Geoemyda* the inner walls of these bladders are covered over with long villi of different forms, and which in some are not confined to the bladders, but enclosed between them over the fold of the upper wall of the cloaca; whereas in all the true Emydes and in the Batagurs their inner walls appear to be smooth.

It is a noteworthy fact that the cloacal bladders do not occur, as far as my researches go, in *Testudo*, *Pyxidea*, *Trionyx*, *Chitra*, and *Pelochelys*. This is a significant circumstance, which suggests the reflection that these bladders are related to the habits of life of the animals possessing them, because on viewing their distribution, as indicated by these observations, it is evident that they are confined to the forms which lead a semiterrestrial and semi-aquatic life, those animals which are essentially terrestrial in their habits and those which are truly aquatic being unprovided with them. It would thus seem, *à priori*, that it is owing to their existence in the Emydes and Batagurs that these forms are endowed with a diversity of habit above their fellows—because there is no very wide line of distinction, apart from these bladders, between the general anatomy of an Emyde and a terrestrial tortoise, beyond perhaps that the lung of an Emyde, like that of a *Trionyx*, is more invested with muscular substance, and the disposition of the nostrils differs somewhat.

These bladders are capacious sacs, opening, as I have stated, on each side of the cloaca, near its anterior extremity; and they occupy the groin and project into the peritoneal cavity, covered, of course, by the peritoneum, and having the lung in certain species lying directly in contact with a considerable extent of their upper border. By the nature of the fold which intervenes between their openings, the portion of the cloaca anterior to them can be shut off by the apposition of the fold to the floor of the cloaca, so that, for the time being, the bladders may be in direct communication with the cloaca, to the complete exclusion of all the other openings except the external anus. These circumstances seem also to favour the supposition that these bladders are in some way functionally related to the aquatic aspect of their existence, since it is an acknowledged fact that some Chelonia draw in and eject water from the cloaca, like the Holothuridæ and other allied in-

vertebrates—an observation which was made by Townson three quarters of a century ago, but which has been verified by other naturalists and what I have myself noticed. Indeed the cloaca in different species of Southern-Asiatic *Emydes* is not unfrequently observed dilated with water, which they squirt out in considerable jets when they retract their limbs and tail, as they generally do when suddenly removed from that medium. Although I have examined, immediately after death, nearly one hundred individuals belonging to those genera which are furnished with cloacal bladders, yet in no instance have the cloacal bladders been distended with water; whereas they have frequently yielded a yellowish grumous substance, most especially abundant in those forms which have these bladders provided with villi. It is also important to note that they are in no way connected with any other viscus, and that their only orifice is in the cloaca. On the other hand, the azygos or partially divided bladder is generally more or less filled, frequently to distention, in animals recently taken from the water, with a clear limpid fluid not pure water. In the *Crocodilia* the equivalents of these pouches are filled with a substance which has the odour of musk; but I have never particularly observed that the *Chelonia* possessing these pouches are more characterized by a peculiar odour than the pouchless forms.

The function, however, which these bladders perform in the economy of the semiterrestrial and semiaquatic *Chelonia* remains yet to be determined by careful observation and experiment.

One observation on the importance of their structures as an indication of the habits of these animals, as illustrated by the genus *Pyxidea*. The form *Pyxidea mouhottii* has been classed with the *Emydes*; but an examination of its cloaca reveals that, unlike those animals, it is unprovided with cloacal bladders. And what are its habits of life? This is a question which I am enabled to answer from the circumstance that I had two specimens under my observation over nine months, during which period they never entered water, and did not exhibit any aquatic tendencies.

All the *Chelonia* of South-eastern Asia which I have examined, belonging to the genera *Testudo*, *Geoemyda*, *Pangshura*, *Emys*, *Batagur*, *Cuora*, *Cyclemys*, *Platysternum*, *Emyda*, *Trionyx*, *Chitra*, and *Pelochelys*, are distinguished by the presence of a pair of peritoneal canals which traverse the cloaca to the base of the glans of the penis and clitoris.

Cuvier* has fully indicated the nature of these canals in the male tortoise; but it is to Is. Geoffroy St.-Hilaire and Martin† that we are indebted for an account of those structures in the female, although some of the results of these observers may not be altogether accepted. Cuvier has described the peritoneal canal of the male as terminating in a *cul-de-sac* at the base of the glans; whereas Is. Geoffroy St.-Hilaire and Martin supposed that they had established a much more intricate arrangement in the female. But before mentioning their views I shall say a few words about the peritoneal canals and their relations.

These canals commence on each side of the pyriform neck of the bladder, within the perivisceral cavity; and they are in reality diverticula for that cavity, being lined with a serous membrane. Each canal begins in the depression or pit in the visceral cavity, external to the neck of the bladder. When distended by a probe, the orifice of the canal (or, more correctly, the diverticulum) is found to have considerable capacity, and to lie along the inside of each corpus cavernosum, at first crossing the spongy bulb of the male organ, and then lying between the corpora cavernosa and in position immediately external to the genito-urinal groove traversing the floor of the cloaca, or in reality the dorsum of the penial tract. In all the foregoing genera these diverticula of the perivisceral cavity are prolonged to the base of the glans, both of the penis and clitoris, and without any apparent diminution in capacity. Isidore Geoffroy St.-Hilaire and J. G. Martin, in examining an example of *Emys trijuga* quite recently dead, state that they perfectly succeeded in injecting the two peritoneal canals with mercury, and that they certainly saw it penetrate into the corpora cavernosa, and also into the small conduits of the glans, which became inflated, rising upwards to a level with the surface of the organ. Moreover they considered that they had established the existence of a communication between the peritoneal canals and the corpora cavernosa, by being able to propel a globule of mercury from the peritoneal cavity either into the little conduits of the glans or into the cavernous bodies, and as by an inverse movement they made the globule reenter into the peritoneal canals. Thus globules contained in the little conduits of the glans, ascending them, might be propelled into the peritoneal canals, thence into the cavernous bodies; and, reciprocally, those

* Anat. Comp. vol. v. p. 114.

† Ann. des Sc. Nat. vol. xiii. (1828) pp. 153, 201.

contained in the corpora cavernosa might be transmitted by the peritoneal canals into the little conduits of the glans, thence into the cavity of the cloaca. They therefore held that the little conduits of the glans were the terminal branches of the peritoneal canals.

They had previously stated that in *Testudo indica** the conduits of the glans terminated near the summit of the clitoris; but from their experiments on *E. trijuga* they found that the orifice of the peritoneal canal terminated nearer to the base of the clitoris than to its summit; and they mention that the position of the opening in *E. trijuga* is intermediate between what they observed in *Testudo indica* and its position in the crocodile, but more resembling the latter, in which the peritoneal canals open at the base of the glans. They arrived, therefore, at the following conclusion—that the peritoneal canals in the tortoise and the crocodile divide at their extremity into two branches, one going to open into the cloaca, and the other tending towards the corpus cavernosum. But according to Is. Geoffroy St.-Hilaire and Martin, there was this important physiological difference—that the second branch opened into the cavity of the corpus cavernosum in tortoises, whilst it terminated in a *cul-de-sac* in the crocodile. I observe that Professor Owen † states that the peritoneal canals of the crocodile, besides communicating with the corpus cavernosum, open outwardly upon papillæ situated on each side of the base of the penis and clitoris, thus conforming, according to his view, with the structure of the tortoises as described by Is. Geoffroy St.-Hilaire.

Having lately directed my attention to these remarkable diverticula from the peritoneal cavity, and finding that my observations on their structure do not agree altogether with either those of Cuvier, Is. Geoffroy St.-Hilaire, or Owen, I shall here record a few of the examinations I made on some species of different genera and of both sexes. Before doing so, I may mention that Is. Geoffroy St.-Hilaire used mercury for his injections; but the membrane lining the walls of these diverticula is so delicate, and mercury so heavy and penetrating, that I am not surprised at the results which he obtained. In injecting the canals I have used only water coloured with a solution of carmine. I was most careful not to

* They were not perfectly satisfied with the identification of the species, but state that the subject of their observation was one nearly allied to *T. indica*.

† Comp. Anat. vol. i. p. 433.

rupture the inner linings by too strong pressure, whilst at the same time I fully distended them.

1st experiment.—This was made on a male of *Geoemyda grandis*. The fluid, injected into the peritoneal canal from about the upper third of the length of the penis, flowed freely through it, appearing at an opening situated immediately at the base of the glans and close to the inside of the genito-urinal groove. Repeated slight pressure was exercised on the dilated canal, and then the corpus cavernosum of its side was laid open to ascertain if any fluid had passed into it; but whilst the interior of the peritoneal canal was richly coloured with the carmine, no trace of colour could be detected in the corpus cavernosum. At the point where the canal terminated externally there were indications of an orifice even before the injection was applied, in the absence of pigment at that point; but I failed to detect any communication between the peritoneal canal and the corpus cavernosum.

2nd experiment.—In a male *Emys Hamiltonii* the coloured injection appeared like a jet from a fine artery, issuing from a very minute orifice in the same position as the orifice of *Geoemyda grandis*; and no trace of carmine could be observed in the corpus cavernosum, or the presence of any orifice leading from one canal to the other.

3rd experiment.—In a male specimen of *Trionyx ocellatus*, in which the penis was very flaccid, the orifices of the peritoneal canals are wide orifices situated more anterior to the base of the glans than in *Emys* and *Geoemyda*, and more on the side of the penis, further away from the urino-genital groove. The mixture flowed through them in a great stream, the penis being that of a much larger animal than any *Geoemyda*. No trace of injection could be found in the corpus cavernosum of the side injected; nor could any orifices be detected, even with the aid of a pocket-lens, between the peritoneal and the corpus cavernosum of the opposite side when they were laid open to near the termination, nor in any other portion of their walls. Moreover, when the corpora cavernosa were injected, no trace of carmine appeared in the peritoneal canals, or at the tips of the lobes of the glans, which are white, and form the termination of the branches of the urino-genital groove.

4th experiment.—In a female of *Trionyx gangeticus* the coloured injection passed at once through the peritoneal canal, appearing at a spot situated some little distance above the base of the glans

and external to the urino-genital groove. No communication could be discovered to exist between the corpora cavernosa, which are very small in the large female.

5th experiment.—A female of *Batagur thurgi* had the orifice situated on a small papilla immediately external to the base of the glans, on the inner margin of the so-called preputial fold or hood of the clitoris; and no trace of communication was discernible between the corpus cavernosum and the canal of the peritoneum.

6th experiment.—In a female of *Chitra indica* the opening of the peritoneal canal was a very minute orifice situated at the bottom of a deep pit with puckered margins, external to the base of the clitoris. The peritoneal canal had its inner walls more or less coloured, near its distal end, with fine dark lines of the same pigment as that of the clitoris itself, thus indicating the continuity of the lining membrane with that of the external surface. The canal was also partially filled near its end with a grumous substance, but quite different from the coagulated blood that filled the corpus cavernosum.

7th experiment.—In a female *Emys trijuga* from Burma, which was rather shrunk from preservation in spirit, the injection would not pass; but when the canal was laid open nearly to its extremity, no difficulty was experienced in passing a fine bristle, which appeared in much the same position as in *Geoemyda grandis*.

8th experiment.—A similar result was experienced in a female of *Testudo platynotus*, Blyth.

9th experiment.—In a female of *Batagur lineatus* the injection passed freely; and the orifice occupied the same place as in *B. thurgi*, and there was no indication whatever of the existence of an orifice between the peritoneal canals and the corpora cavernosa.

10th experiment.—*Platysternum megacephalum* and *Cyclemys dentata* were so hardened and shrivelled by spirit that no orifice for the well-developed canals could be detected.

I should have been more satisfied with these experiments had I succeeded in passing the injection freely through the peritoneal canals of all the species examined; but I attribute my want of success in these two instances chiefly to the circumstances that the parts were hardened and contracted with spirit, and that the orifices were very minute. I am not prepared, however, to go the length of saying that there is invariably a communication between the peritoneal canals and the cloaca in the males; but at the same time there can be no doubt that in the males of *Geo-*

emyda grandis, *Emys Hamiltonii*, and *Trionyx ocellatus* such a communication does exist. In this respect these animals conform to the course of these canals in the crocodile. Now *Geoemyda grandis* and *Trionyx ocellatus* belong to two widely separated groups of Chelonia; and the fact that the peritoneal canals open into the cloaca in both would lead us to anticipate that this arrangement was common to all the Chelonia which resembled them in habits of life and general structure. But a more extended series of experiments will be necessary to establish this point; and all I insist on is, that in the males, as in the females, experimented upon these canals do open into the cloaca, and in this respect conform to the general type of structure distinctive of the peritoneal canals of Crocodilia, and of the so-called abdominal pores of the Cyclostomous and Ganoid fishes.

But the view of the structure of these canals to which I wish to direct more particular attention is, that in the foregoing experiments no trace of any communication between the peritoneal canals and the corpora cavernosa could be observed. I was at first very sceptical regarding the results I had obtained, after the very emphatic statement of Is. Geoffroy St.-Hilaire, that in his experiments on *Emys trijuga* the mercury injected flowed freely between the peritoneal canal and the corpora cavernosa and *vice versá*, and from the glans into the peritoneal canal; but as my experiments were conducted with great care, I have thought it well to record them, because there are great difficulties in accepting Is. Geoffroy St.-Hilaire's explanation of the relations which, he states, subsist between the peritoneal canals and the corpora cavernosa. In claiming for the peritoneal canals the existence of a series of minute sieve-like orifices intervening between them and the corpora cavernosa, he would thus establish a direct communication between the blood-vascular system and the peritoneal cavity—a condition of things which would be unique in the animal kingdom. Moreover, as he adduces the passage of the mercury as a proof of the existence of these orifices between the large blood-conduit, the corpus cavernosum and the peritoneal canal, we are led to suppose that the blood would follow a similar course, which means that it passes backwards and forwards over the serous or peritoneal lining of the canal and the structurally different inner wall of the corpus cavernosum. Such a view of the relation of these two canals is opposed to the first principles of physiology. Is. Geoffroy St.-Hilaire was quite aware of these practical difficulties to the acceptance of the

view which he had propounded regarding the relations of these structures, and he remarks that he had never observed blood in the peritoneal canal; but to account for this, he conjectured that the supposed minute orifices leading into the corpora cavernosa were related to the cavity of that tube much in the same way that the openings of the seminal tubes are to the urethral canal of the higher vertebrates, the orifices of which are so protected that the urine in its passage outwards is efficiently denied access to them. This comparison leads to the supposition that their orifices exist only for the transmission of fluid from the peritoneal canal to the corpora cavernosa, which would remove one aspect of the difficulty. But as there is no analogy between the closed spongy substance of the glans which is directly continuous with the corpora cavernosa into which the blood-vessels pour the fluid, and the excreting tract of the urethra, the theory implied in the comparison instituted by Is. Geoffroy St.-Hilaire, that a fluid passes from the peritoneal canals into the corpora cavernosa, is a practical difficulty of the greatest moment. What is the fluid which would so pass? If, as he allows, there exists in the female tortoise a direct communication between the peritoneal canals and the cloaca, and, as I have proved, in the male *Geoemyda grandis* and *T. ocellatus*, as these orifices are not valvular, the likelihood is, that as the cloaca is distended with water this fluid finds its way into those canals, it may be even into the peritoneal cavity; and we should thus have to accept the conclusion that the fluid they transmit to the corpora cavernosa, and thus to the blood, was partly composed of the secretion of the peritoneal cavity diluted with water.

It is unnecessary to say any more regarding these views, my purpose not being controversy, but merely to direct more attention to the structures which have, doubtless, an important bearing on the economy of these remarkable animals. My own opinion is that they are in no way related to the generative functions, but that they are, as has been suggested by Duméril and Bibron*, probably accessory and subordinate to transpiration, admitting water into the peritoneal cavity, which adapts the animal to the change to which it is subjected when exposed to the air in too high or too dry a temperature.

Little or nothing is known regarding the development of these canals in the Chelonia; but as they have associated with them in the adult condition a pair of generative tubes and well-defined

* Erpét. Gén. vol. . p. 195.

ureters opening by distinct orifices into the cloaca, they have probably an origin quite distinct from the Müllerian ducts; and the likelihood is that they are strictly homologous with the abdominal pore of the Selachians and Ganoids. The true nature and origin of these pores is little understood; but Mr. F. M. Balfour* has suggested that they are probably the openings of a pair of segmental organs. Embryology, however, must be the ultimate interpreter of their origin and meaning.

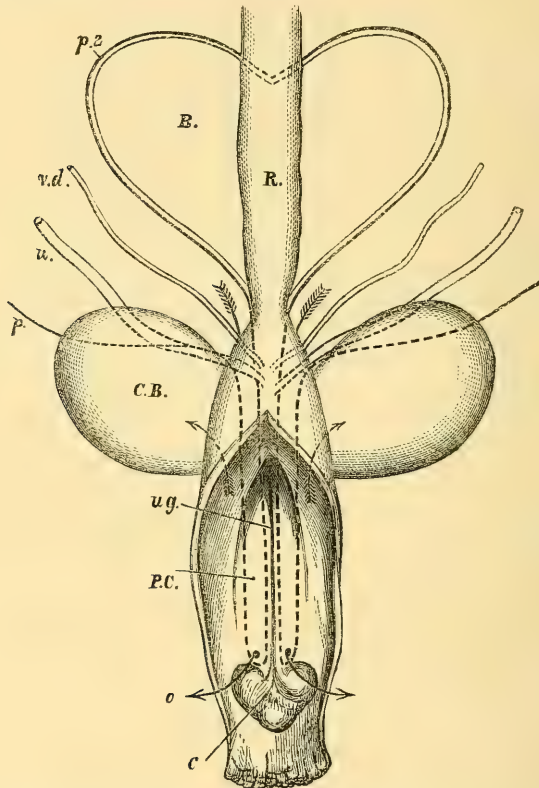


Diagram illustrating the cloacal bladders and the peritoneal canals of Chelonia.

B, urinary bladder; R, rectum; C. B, cloacal bladder (arrows are represented on either side entering these from the cloaca); P. C, peritoneal canals (arrows descend and have exit therefrom at *o*, orifice); *p*, peritoneum; p^2 , peritoneal covering of bladder; *u*, ureter; *v. d.*, vas deferens; *ug*, urinogenital groove; *c*, clitoris.

* Journ. Anat. Phys. vol. x. pt. 1, 1875, p. 34.